The role of the feeding migration and diet of Atlantic salmon (*Salmo salar* L.) in yolk-sack-fry mortality (M74) in the Baltic Sea

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Academic dissertation

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Cover picture: A photo by Markku Saiha: Fishing vessel Eknö drift-netting salmon at the Gotland Deep
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To Anni and Max

One pictures the salmon smolt, after its two years of experience in the river, making its plunge into the great unknown sea. It is still but a little fish, and its instinct calls it to make this great adventure, to visit this vast trackless ocean where go the ships and that great leviathan. It is not tied down to times and seasons, it can make a long or a short stay in the sea, it can roam widely or it can hunt its food near at hand. But there are certain things it will not do. It will not go back to the river in a few months as sea trout would do, it insists on a year of wandering at the least, and it may stay much longer. It will not hang about river mouths as those trout do, or make frequent spawning trips up rivers. It will come in from the sea in good time to answer the call of sex, but it is not going to have this interfere with its life as a rover, with its hunt after good living among the shoals of herring and sprats and sand-eels, and its explorations of this great space where there is so much adventure.

W.L Calderwood, I.S.O., F.R.S.E. (1930)

Contents

Original publications

The thesis is based on the following papers

I. Ikonen, E and Vuorinen, P.J. 2005. Does the choice of feeding area of Atlantic salmon (*Salmo salar* L.) account for differences in offspring mortality (M74-syndrome) in the Baltic Sea. *Submitted*.

II. Ikonen, E. and Parmanne, R. 1992. Possible interactions between salmon migrations and landings, smolt production, herring abundance, and hydrographic factors in the Gulf of Bothnia, 1976–1990. *ICES mar. Sci. Symp*. 195: 492–498.

III. Kallio-Nyberg, I. and Ikonen, E. 1992. Migration pattern of two salmon stocks in the Baltic Sea. *ICES J. mar. Sci*. 49: 191–198.

IV. Karlsson, L., Ikonen, E., Mitans, A. and Hansson, S. 1999. The diet of salmon (*Salmo salar*) in the Baltic Sea and connections with the M74 syndrome. *Ambio* 28: 37–42.

V. Hansson, S., Karlsson, L., Ikonen, E., Christensen, O., Mitans, A., Uzars, D., Petersson, E. and Ragnarsson, B. 2001. Stomach analyses of Baltic salmon from 1959–1962 and 1994–1997: possible relation between diet and yolk-sac-fry mortality (M74). *J. Fish Biol*. 58: 1730–1745.

VI. Ikonen, E. and Torvi, I. 1999. Why were the effects of M74 mortality not visible in the spawning run of Baltic Salmon in 1997 in the Gulf of Bothnia. *Boreal Env. Res*. 3: 421–422.

Author's contribution

The author of this thesis has contributed to the original papers as follows:

Paper	I	II	III	IV	V	VI
Original idea:	EI	EI	EI	LK EI	LK EI	EI
Design and methods used:	EI PJV	EI RP	EI IK-N	LK EI	LK, EI SH	EI IT
Data gathering and processing	EI PJV	EI RP	EI IK-N	EI LK AM	EI, LK, SH, DU, OC, AM, EP, BR	EI IT
Manuscript preparation	EI PJV	EI RP	IK-N EI	LK, EI, AM	SH, LK, EI, AM, OC	EI IT

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Abstract

Atlantic salmon (*Salmo salar* L.) populations exist in about 80 rivers draining to the Baltic Sea. Salmon reproduction has ceased in many rivers due to anthropological changes in river conditions and in some cases salmon stocks have been lost due to overfishing. To compensate for losses in smolt production, large-scale smolt releases into rivers have been carried out since the 1950s in the Baltic Sea area. In 2004, 7.1 million salmon smolts initiated their migration from the river mouths to the sea, of which 75% originated from hatcheries and the remainder were of wild origin. The rearing of salmon in most of the hatcheries around the Baltic Sea has been based on eggs obtained from ascending, feral spawners. However, in Finland captive spawners have been used almost exclusively to supply the eggs, while feral spawners have only been used to renew brood fish in hatcheries.

In 1974, in a Swedish salmon hatchery, exceptionally high yolk-sac fry mortality was observed. The mortality was recorded only within a few family groups, while the others were viable. As no causative factors were found in the hatchery or in rearing practices, it was concluded that the syndrome must be related to nutritional factors in the sea environment from where the spawners ascended the river. Therefore, it was named as M74 syndrome. The letter M came from the Swedish word miljörelaterad, meaning environmentally caused, and 74 was the year (1974) when the syndrome was first detected. The syndrome has since been detected in the salmon populations ascending the rivers draining into the Gulf of Bothnia and Gulf of Finland, but not in the Baltic Proper rivers, except in the River Mörrumsån in southern Sweden.

The M74 syndrome has always only been detected in a proportion of the females in different spawning populations. The syndrome strengthened rapidly in early 1990s, but almost disappeared during the early 2000s. These findings gave rise to the hypothesis that the M74-positive salmon had fed on different food compared to healthy ones. Therefore, I investigated the distribution pattern of salmon in the feeding areas and their diet in these areas. I also sought to determine causative factors in the food.

Moreover, I have studied the migration patterns of salmon postsmolts with tag recovery data and the possible biotic and physical factors affecting the selection of feeding areas. Those areas where salmon perform their feeding migrations have been determined with the aid of salmon smolt tagging data by mapping the tag recoveries of feeding fish. I have also used the distribution of offshore catches to determine the feeding area selection. Stomach analyses of feeding salmon caught in different areas have used to reveal differences in food composition.

The selection of the feeding area might take place during postsmolt migration, which is strongly guided by thermal zones in the inshore areas. It appears that during postsmolt migration, an abundant availability of fish of an edible size, such as 0+ herring, causes postsmolts to stop their further migration, and the actual feeding migration is then mainly guided by movements of prey fish shoals. Salmon populations in the rivers draining into the Gulf of Bothnia migrate to the southern Baltic

Proper to feed, but during some years more feeding takes place in the southern basin of the Gulf of Bothnia (Bothnian Sea) and the northern Baltic Proper.

Stomach sampling suggests that salmon prey species in the central and southern Baltic Proper are sprat (*Sprattus sprattus* L.), herring (*Clupea harengus* L.) three-spined stickleback (*Gasterosteus aculeatus* L.) and sandeel (*Ammodytes* sp.) in order of importance. In the northern Baltic Proper, Bothnian Sea and Gulf of Finland, salmon prey dominantly on herring followed by stickleback and to a minor degree on sprat.

The analysed data suggest that when the feeding migration of salmon is emphasized in the northern Baltic Sea, an increased proportion of M74 spawners in the rivers follows, and vice versa. It seems that a diet dominated by herring is a causative factor for M74 syndrome in the northern rivers. It might also be so that the causative factor is not species related but the reason could be found in the food web of salmon. In the northern Baltic Sea the composition of plankton species available for herring differs from that occurring in the central and southern Baltic Proper.

A deficiency in thiamine, which has been shown to be the main reason for the syndrome, may be a result of a herring-orientated diet. Thiaminase activity is probably higher in herring than in sprat, and thus the thiamine stores of ingested herring are destroyed faster in the salmon stomach. In addition to a herring-dominated diet, a further reason may also lie in the food of salmon prey species. Small limnic plankton species dominate in the northern feeding areas, while in the southern areas larger neritic species are common. Poor nutritional conditions in the northern Baltic Proper were reflected in a retardation of herring growth beginning in the early 1980s and even more profoundly after the late 1980s, when the annual growth of sprat also decreased. There are indications that the neritic plankton species are better food for herring and sprat, containing more carotenoids than limnic ones and probably also a greater thiamine content.

The M74 syndrome detected in the Gulf of Finland salmon populations seems to fit the same possible explanations. Those salmon feeding in the Gulf of Finland and northern Baltic Proper have suffered from the syndrome, while salmon migrating to more southern areas have produced viable offspring. Latvian and Polish salmon have not suffered from the M74 syndrome, even though at least a certain proportion of postsmolts migrate to the northern Baltic Sea. However, it is probable that later migration to the more southern areas and the different diet there prevents the emergence of the syndrome. The syndrome detected in the River Mörrumsån might also be related to the northern feeding areas of its salmon population. However, no detailed data on the feeding migration of this salmon strain are available.

In the future, the factors leading to a strengthening of M74 mortality are still likely to exist. An increased proportion of feeding salmon in the northern Baltic Sea might result in a growing number of M74-positive females in the spawning populations. However, possible improvement in the salmon food web in the northern Baltic Sea might diminish the negative effect of feeding in the north.

1. Introduction

1.1. Salmon rivers

Atlantic salmon (*Salmo salar* L.) enter about 80 rivers emptying into the Baltic Sea. There are 39 rivers in which salmon spawn and produce offspring. Self-sustaining salmon populations exist in 27 rivers. Natural reproduction also occurs in 12 other rivers due to annual smolt or parr releases. In the rest of rivers with a salmon run, dams prevent entry to the reproduction areas. Salmon entering these rivers mainly originate from smolt releases in the river mouth (ICES, 2005b) (Fig. 1).

Salmon terminology (Allan and Ritter, 1977) used in this thesis is presented in the following table.

Stage	Term	Definition
1	Alevin	The stage from hatching to the end of dependence on the yolk sac the primary source of nutrition.
2	Fry	Stage from independence of the yolk sac as the primary source of nutrition to dispersal from the redd.
3	Parr	Stage from dispersal from the redd to migration as a smolt. The parr stage lasts 1–4 years in the Baltic Sea rivers.
4	Smolt	Fully silvered juvenile salmon migrating to the sea.
5	Postsmolt	Stage from departure from the river until the end of the first winter at sea (in this thesis until the end of the following April).
6	Salmon	After the first winter at sea.

In 2004 a total of 7.1 million smolts originating either from natural reproduction (25%) or released from hatcheries initiated their sea migration from Baltic Sea rivers (ICES, 2005a).

In the **Gulf of Bothnia** there are in total 13 salmon rivers with natural smolt production. These rivers produced 1.53 million wild smolts in 2004. In addition to this, hatchery-reared smolts are annually released into former salmon rivers, which in 2004 totalled 3.38 million smolts. Salmon smolt production in the Gulf of Bothnia accounted for 71% of the total smolt production in the Baltic Sea in 2004 (ICES, 2005a).

In the **Gulf of Finland** salmon reproduction occurs in 12 other rivers, but mainly based on annual smolt or parr releases. In 2004 these salmon rivers produced 11 000 wild smolts. In addition to this, annual hatchery-reared smolt releases take place, which in 2004 totalled 820 000 smolts. Salmon smolt production in the Gulf of Finland accounted for 12% of the total smolt production in the Baltic Sea in 2004 (ICES, 2005a).

In the **Baltic Proper there** are 14 salmon rivers with natural smolt production, including three rivers with annual enhancement releases. In 2004 these 14 rivers produced 63 000 smolts (ICES, 2005a). In addition to this, annual hatchery-reared smolt releases take place, which in 2004 totalled for 1.08 million smolts. Salmon smolt production in the Baltic Proper accounted for 17% of the total smolt production in the Baltic Sea in 2004 (ICES, 2005a).

1.2. Salmon fishing

Commercial salmon fishing is carried out either in the offshore areas harvesting feeding salmon or inshore during the spawning migration. Offshore fishing operates with drift nets or drifting long lines while in coastal areas migrating salmon are mainly caught by trap nets (Christensen and Larsson, 1979; Christensen *et al*., 1994). Catch figures indicate that offshore catches have decreased especially in the Gulfs (Fig. 2) (ICES, 2005a). Recreational salmon fishing is mainly carried out in rivers or river mouths by angling and in inshore and offshore areas by trolling. The total salmon catch in 2004 was 2017 tonnes. However, catches have earlier been considerably higher. The highest recorded catch (5636 tonnes) was taken in 1990. The long-term average catch (1972–2004) is 2996 tonnes (ICES, 2005a).

1.3. Migrations

Salmon from the Gulf of Bothnia rivers migrate

Fig. 1. The Baltic Sea and the rivers producing salmon smolts or where smolts have been introduced.

as postsmolts to feed principally in the Baltic Proper, but during some years the proportion of feeding fish has increased in the southern part of the Gulf of Bothnia (Bothnian Sea) (I, II, III), (Carlin, 1969; Christensen and Larsson, 1979; Ikonen and Auvinen, 1984; Aro, 1989; Salminen *et al.*, 1994; Karlsson and Karlström, 1994). The majority of salmon originating from the Gulf of Finland feed in the Gulf and to lesser extent migrate to the Baltic Proper (III), (Ikonen and Auvinen, 1984; Kazakov, 1985). Salmon inhabiting the rivers draining to the Baltic Proper feed mainly in the Baltic Main Basin, but migration to the Gulf of Finland and to some extent to the Gulf of Bothnia also occurs (Alm, 1934; Carlin, 1969; Mitans, 1970; Larsson and Persson, 1981;

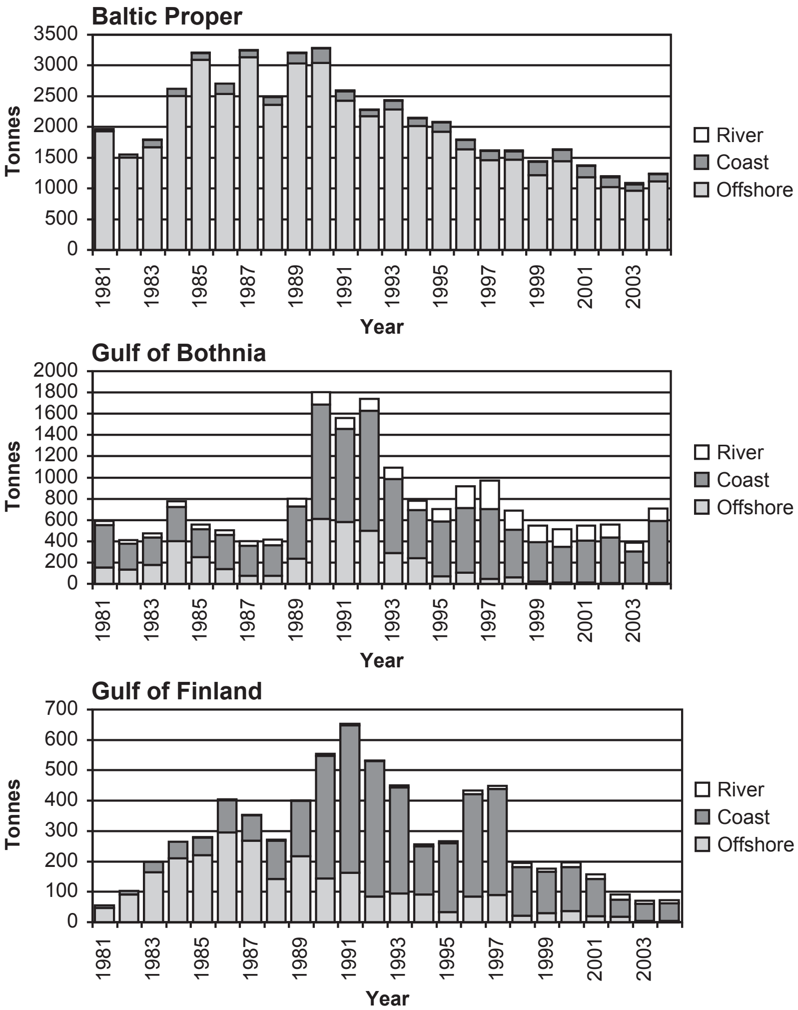


Fig. 2. Salmon catches in offshore, coastal and river fishing in the Baltic Sea in 1981–2004 (ICES 2005a).

Bartel, 1987; Bartel, 2001). The Gulf of Riga has no role as feeding area for salmon (Karlsson *et al*., 1995).

1.4. Salmon feeding

Salmon postsmolts feed on terrestrial insects at the beginning of their marine phase (Alm, 1934; Lindroth, 1961; Power, 1969; Mitans, 1970; Jutila and Toivonen, 1985; Salminen *et al*., 1994), but shift to predation on fish when they reach a length of 25–30 cm (Thurow, 1966; Salminen *et al*., 2001). In the Baltic Proper the dominant food is sprat followed by herring, stickleback and sandeel (Christensen, 1961; Thurow, 1966; Christensen and Larsson, 1979), (IV, V). The proportion of sprat in the diet of salmon is small in the Gulf of Finland (Andersson, 1980) and almost negligible in the Gulf of Bothnia (V). In the northern Baltic Proper as well as in Gulf of Bothnia and Gulf of Finland, herring dominates in the diet followed by stickleback (Salmi and Ikonen, 1982; Ikonen, 1995; Salminen *et al*., 2001), (V).

1.5. The M74 syndrome

The M74 syndrome (mortality of yolk-sac fry) was first described by Norrgren *et al*.(1993). It was observed that some family groups in salmon hatcheries had high mortality rates. The mortality was believed to be caused by environmental factors, and was therefore named the M74 syndrome (M stands for "miljörelaterad", meaning environmentally-caused, and 74 is year when the syndrome was discovered).

A deficiency of thiamine has been demonstrated to be the main factor in the etiology of the M74 syndrome (Koski *et al*., 1999; Amcoff, 2000; Keinänen *et al*., 2000; Koski, 2004). Fisher *et al*. (1996) and Fitzsimons *et al*. (1999) have shown that thiamine deficiency also resulted in the Early Mortality Syndrome (EMS) in the Great Lakes and the Cayuga Syndrome in the Finger Lakes in New York State.

The syndrome has created problems in the Gulf of Bothnia and Gulf of Finland in fish hatcheries that depend on feral spawners to supply eggs for smolt rearing. However, captive spawners, fed with artificial food, have not suffered from the syndrome. Neither have salmon strains feeding outside of the Baltic Sea shown any symptoms of the syndrome (Amcoff *et al*., 1999; Koski *et al*., 2001). The syndrome has been detected in wild salmon populations in the Gulf of Bothnia and in the Gulf of Finland, but in the Baltic Proper only in the River Mörrumsån. When the mortality rates were at their highest in the 1990s, hatcheries suffered from a shortage of rearing material due to the high yolk-sac fry mortality. The syndrome also affected the self-sustaining salmon populations so strongly that it was detected in decreased parr densities in nursery areas (Karlström, 1999). Therefore, it is of great importance to know the mechanism underlying the syndrome. For salmon rearing and fishery management purposes it would be very beneficial if the variation in the syndrome could be forecasted.

2. The aim of the present study

The main goal of the present study was to examine possible reasons for the M74 syndrome. In particular, I have sought to answer the question of why the same spawning population can have females producing offspring that die due to M74 syndrome, but also females that produce viable offspring.

M74-positive females have shown a lower thiamine content both in muscle tissue and eggs compared to healthy ones. A pale muscle and egg colour suggests a decreased intake of carotenoids. Additionally, higher concentrations of dioxin-like organochlorines (OCs) were measured in the M74-positive females. Different carotenoid levels and differences in concentrations of dioxin-like organochlorines indicate difference in diet between M74 positive and negative salmon. Therefore, because salmon are opportunist in feeding, utilising available prey species, I have investigated the selection of feeding areas (I, II and III) and salmon diet there (IV and V).

The second question I have raised is why there have been parallel changes over time in the proportion of M74-positive female salmon in spawning populations from separate rivers, from < 1% to 95%. The effect of feeding area on the M74 syndrome was examined with aid of Carlin tagging data in which the location of tag recoveries of feeding salmon originating from the Rivers Oulujoki, Iijoki, Simojoki, Kemijoki and Tornionjoki indicate the choice of feeding area (I). Catch statistics for feeding salmon caught by offshore fishing were also used to determine the choice of feeding area between the Baltic Proper and Bothnian Sea (I, II). The proportion of tag recoveries or nominal catches of feeding fish either in the Baltic Proper or in the Bothnia Sea have been compared with the proportion of M74-positive female salmon in the spawning populations. Additionally, I have studied the association between distribution of tag recoveries in the Baltic Proper (northern or southern part) and the M74 syndrome in the home rivers (I).

The third question I have addressed is **why the syndrome has not occurred in the salmon populations originating from the rivers draining into the Baltic Proper, except in the River Mörrumsån, and why the syndrome in Gulf of Finland rivers has been weaker than in the Gulf of Bothnia**. In this thesis and in papers II, III and I have investigated the distribution patterns of salmon in the areas where they feed.

I have also tried to find an answer to **question of whether the syndrome is related to the prey species or the food of the prey species**. The diet of feeding salmon differs in separate feeding areas. In the central and southern Baltic Proper sprat dominates in diet, but northwards from there the importance of sprat decreases so that herring dominates in northern Baltic Proper, in the Gulf of Bothnia and the Gulf of Finland (IV, V).

Are salmon of hatchery origin more vulnerable to the syndrome than those originating from natural spawning? The occurrence of the syndrome in the wild salmon catches has been examined from catch samples taken during spawning migration (VI).

3. Material and methods

Salmon hatchery strains discussed in the thesis consist of reared salmon from the Rivers Oulujoki, Iijoki and Kemijoki (I). In the River Kymijoki, the salmon strain used originates from the Russian river Neva, from where it was imported in the 1970s (III). Two other strains originate from the Rivers Tornionjoki and Simojoki, in which salmon populations are at present self-sustaining (I), (ICES, 2005a).

Tagging data used in this thesis are based on tag recoveries of either hatchery-reared or descending smolts trapped and tagged during the smolt run. Such tagging was carried out in the Rivers Tornionjoki and Simojoki. Tag recoveries are held in a database maintained by the Finnish Game and Fisheries Research Institute.

I have investigated the distribution of postsmolts from the river mouths to the feeding grounds on the basis of tag recovery data. In this analysis I have combined the tag recoveries of postsmolts from the Rivers Tornionjoki, Kemijoki, Simojoki, Iijoki and Oulujoki and followed migration from the descent to sea in May until the end of the postsmolt phase in April of the following year. The distribution is presented in two-month periods (Fig. 3a–f).

Catch statistics are based on data collected by the International Council for the Exploration of the Sea (ICES, 2004). The salmon diet data from the late 1990s are based on stomach sampling presented in papers IV and V.

M74 mortality figures are partly based on unpublished data collected by Pekka Vuorinen (Finnish Game and Fisheries Research Institute) and partly on published data (Amcoff, 2000; Keinänen *et al.*, 2000; ICES, 2005a).

Tagging data used in the analyses have been gathered with the aid of both professional and recreational fishermen who have sent recovered tags to the Finnish Game and Fisheries Research Institute. On the basis of tag recovery data it is possible to map the migration routes and feeding areas of salmon. However, the method describes the situation only in areas where fishing has been performed. It is quite probable that the recoveries do not describe all the areas where salmon migrate due to the low intensity of fishing or use of fishing methods unable to catch salmon. This is especially the case when the postsmolt migrations are studied on the basis of tagging. The minimum landing size of 60 cm and the closed period for long lining (1 April–15 November) (International Baltic Sea Fishery Commission, 2005) have channelled fishing methods so that smaller salmon are seldom caught in offshore fishing. Trap net fishing of herring or pelagic trawling directed to herring and sprat also catch salmon postsmolts to some extent, but these postsmolts are difficult to find among the herring and sprat due to the large catch volume.

However, the location of salmon offshore fishing is influenced by the abundance (catch per unit of effort, CPUE) of fish in different areas (Christensen and Larsson, 1979). In practice, fishermen have tried target their fishing at the areas with the highest abundance of salmon. This has been based on mutual cooperation (telephone) between offshore fishing fleets during fishing to find the fishing areas where the abundance of salmon is satisfactory. Therefore, the tag recoveries are mostly located in the best feeding areas. Naturally, there are feeding salmon outside of these best areas, but it could be presupposed that the importance of these areas as feeding grounds is smaller. The mobility of offshore fishing was evident in the mid-1970s when the abundance of feeding salmon increased in the Bothnian Sea and Danish fishermen came from the southern Baltic Proper to the Bothnian Sea to fish (Christensen and Larsson, 1979; ICES, 2005a). Therefore, feeding areas could also be quite reliably located on the bases of offshore fishing.

Salmon fishing that harvests homing salmon is carried out by fixed trap nets. It is quite obvi-

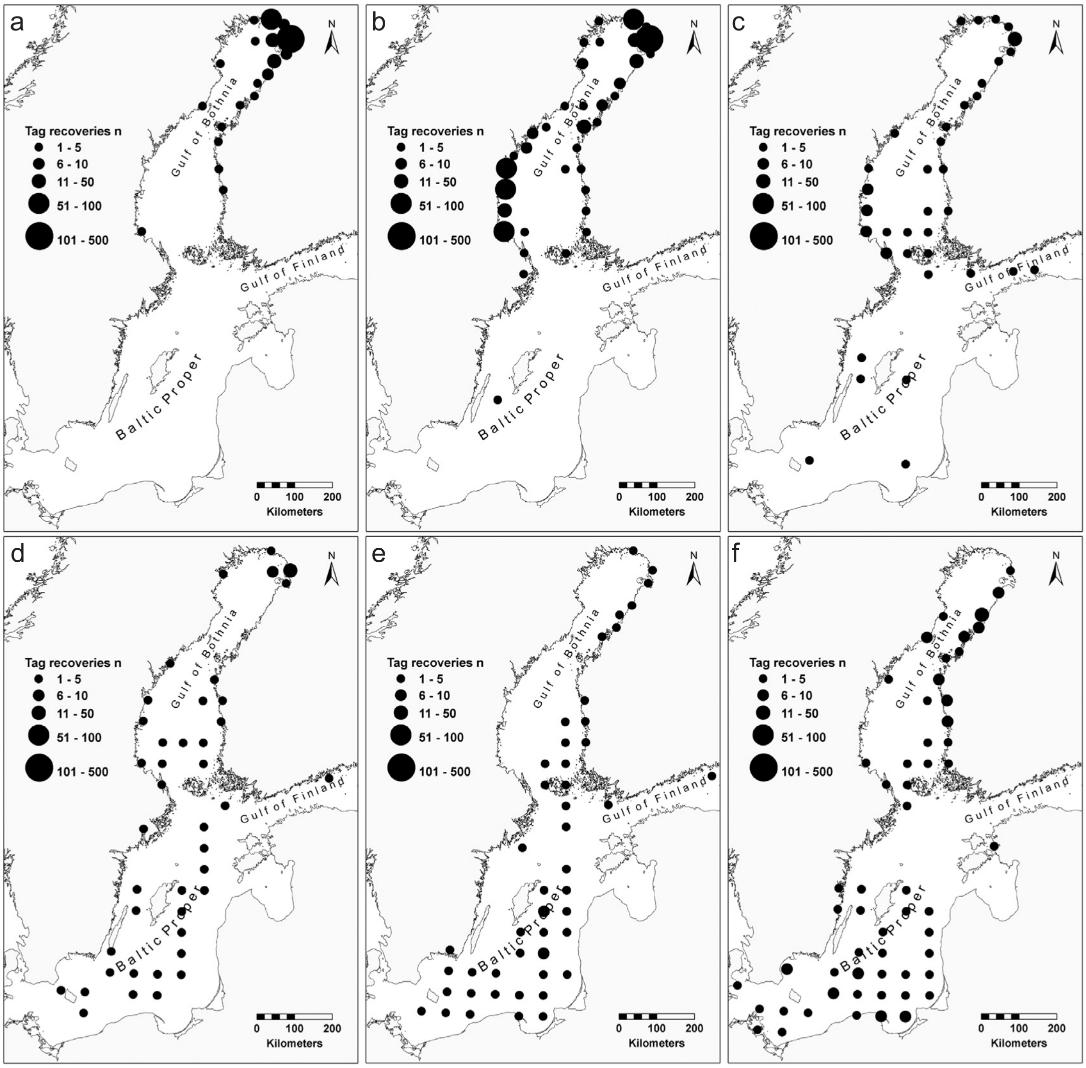


Fig. 3. Tag recoveries of salmon postsmolts tagged in the smolt phase in the Rivers Tornionjoki, Kemijoki, Simojoki, Iijoki and Oulujoki in 1959–2002. (**a**) tag recoveries in May–June n = 882, (**b**) tag recoveries in July–August n = 436, (**c**) tag recoveries in September–October n = 172, (**d**) tag recoveries in November–December n = 139, (**e**) tag recoveries in January–February n = 112, (**f**) tag recoveries in March–April n = 167.

ous that tag recoveries of homing salmon caught by trap nets cannot precisely locate migration routes in all cases. However, the long tradition in this fishing has enabled fishermen to locate their gear so that in most of cases it harvests the biggest possible proportion of migrating salmon passing a particular location. Therefore, the tag recoveries of this fishing locate quite well the main migration routes of salmon.

M74 data are from nine Swedish salmon rivers, a Finnish-Swedish river (River Tornionjoki) and two Finnish rivers. The data used include the proportion of M74-positive females in hatcheries (Sweden) or in experimental incubation (Finland). In 1997–2003 there was a tendency for M74-mortality to be higher in Finland than in Sweden. Partly the difference arises from the fact that in Finland the development of yolk-sac fry is monitored for a more extended period as day-degrees so that milder, later-appearing M74 cases are also registered (ICES, 2005b). Unfortunately, the M74 data are not available from the salmon populations entering to the Rivers Oulujoki, Iijoki and Kemijoki, which have been used in the analysis of migration patterns (I). However, the migration behaviour of salmon in these five rivers seemed to be very similar. The tagging data from the Swedish rivers was not available. Therefore, a comparison of the migration pattern between Finnish and Swedish rivers is not possible. However, the environments of Swedish and Finnish postsmolts are quite alike, and occasionally a significant proportion of salmon originating from the Swedish and Finnish rivers have been reported to feed in the Bothnian Sea instead of migrating to the Baltic Proper (Olofsson, 1926; Järvi, 1938). Svärdson (1955) also reported a marked tendency for salmon in the Swedish rivers to react with the same trend to certain factors.

The effects of the M74 syndrome on the year class strength of wild salmon have been studied on the basis of catch samples collected during the spawning migration (VI).

4. Results and discussion

4.1. Migrations

4.1.1. Distribution of salmon from the rivers in the Gulf of Bothnia to the feeding areas

Salmon smolt migration to the sea takes place in the Gulf of Bothnia rivers in May–June–July, lasting about four to six weeks (Haikonen *et al*., 2005; Jutila *et al*., 2005). Jutila *et al*. (2005) have shown that in the River Simojoki, smolt migration peaks when the river temperature reaches 10 °C. However, the migration of individual smolts begins earlier. In the River Tornionjoki, which is about 500 km long (north–south direction), migrating smolts have been detected in the river when the water temperature has been 5 °C (Haikonen *et al*., 2005). It is usual that when the river temperature has reached 10 °C the sea surface temperature is still low, and drifting ice is occasionally still present at sea (Jutila *et al*., 2005).

The tag recoveries of the postsmolts from the rivers Tornionjoki, Kemijoki, Simojoki, Iijoki and Oulujoki (Fig. 3a–f) suggest that migration follows the Finnish coast in the northern part of the Gulf of Bothnia (Fig 3a). The heating and cooling of the sea surface occurs more rapidly along the shallow coastline than in the open sea. Thus, bands of warm and cold water generally occur along the coasts during the summer and winter, respectively. These are clearly separated from the open-sea water and may suppress the exchange between different zones (Kullenberg, 1981). Temperature may act on a fish through two channels, through sensory receptors and thus the central nervous system, or by a more direct action on metabolism (Harden Jones, 1968). Fish can detect small temperature gradients of even 0.03 °C (Bull, 1936) ref. (Harden Jones, 1968). According to Laevastu (1993), temperature can affect the food requirements and uptake and growth rate as well as swimming speed. At low temperatures (1– 5 °C) the rate of digestion appears to be the chief factor limiting food consumption, with a concomitant reduction in appetite (Brett, 1979). Therefore, postsmolts utilize these warmer thermal channels along the coasts when migrating southwards. In the Bothnian Bay the current along the Finnish coast transports warmer surface water from the south. Therefore, postsmolts migrate along an increasing temperature gradient (Fig. 4). On the Finnish side of the Northern Quark, the Vaasa archipelago (Fig. 1), which stretches almost to the midpoint of the Quark, guides postsmolts far from the mainland to the middle of the Quark. The current from the Bothnian Sea coast also turns west due to the Vaasa archipelago and also to the Coriolis force. Therefore, this thermal channel, leading to the west coast of the Bothnian Sea, forms a natural continuation of the migration route south along the Swedish coast of the Bothnian Sea (Fig. 3b).

The thermal channel on the east coast of the Bothnian Sea could also form a migration route. However, the tag recoveries of postsmolts (Fig. 3b) suggest less usual migration along the east coast compared to the west coast (Fig. 5a).

Postsmolts enter to the Bothnian Sea in July and August (Fig. 3b). In September and October some postsmolts reach the northern Baltic Proper (Fig. 3c) and by the end of the year a great proportion of postsmolts are distributed in the offshore area in the Bothnian Sea and Baltic Proper (Fig. 3d). The migration route in

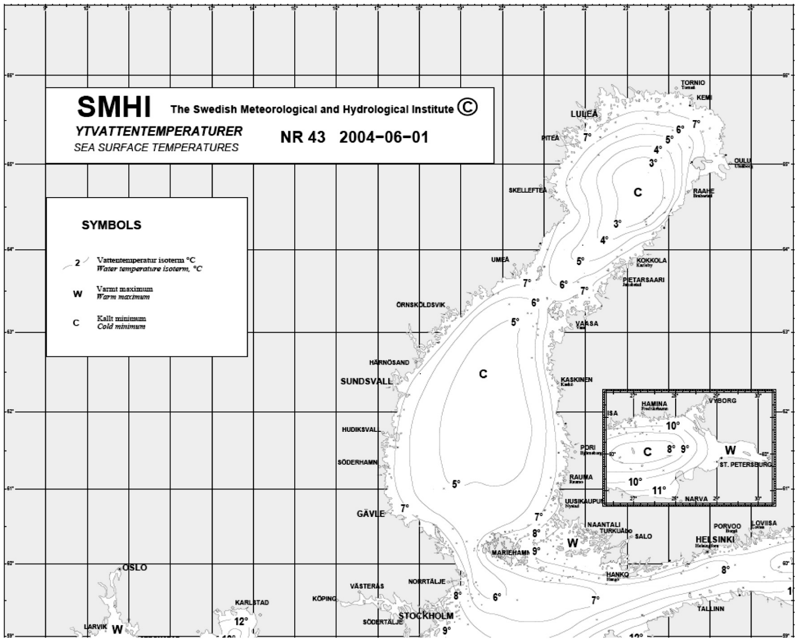
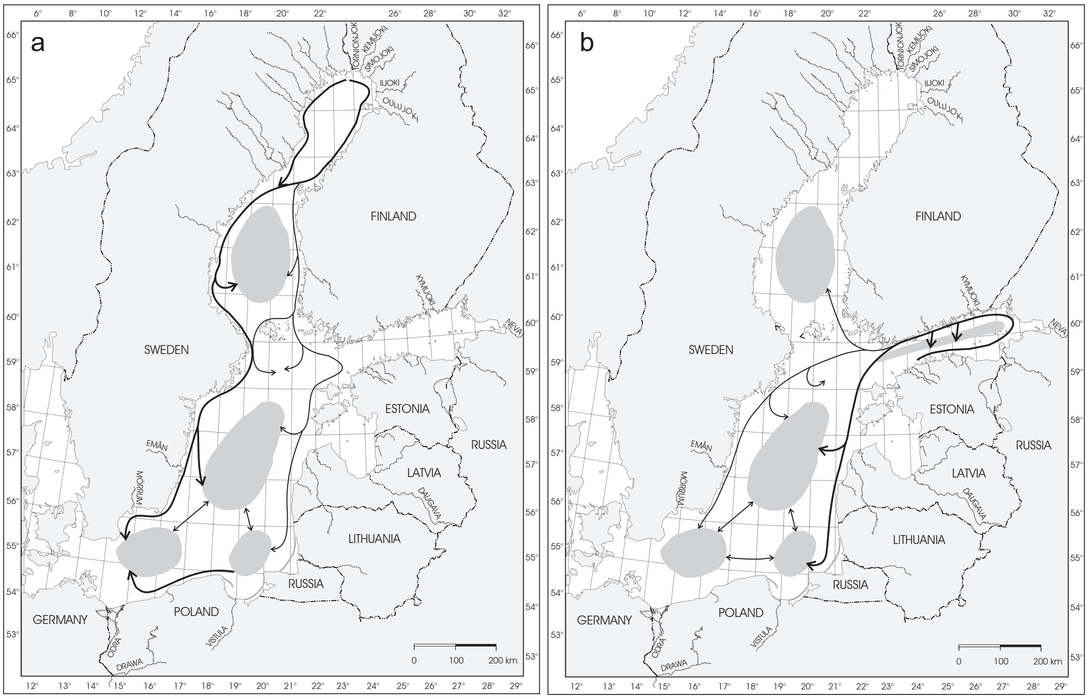


Fig. 4. Sea surface temperatures in the Gulf of Bothnia on 1 June 2004 according to the Swedish Meteorological and Hydrological Institute (SMHI, 2005).

the Baltic Proper cannot be estimated according to tag recovery locations due to the lack of fishing capable of catching migrating postsmolts (Fig. 3d). In January and February (Fig. 3e) and in March–April (Fig. 3f), tag recoveries are obtained from the southern Baltic Proper and also from the Gulf of Bothnia, where the majority of recoveries are obtained in the inshore area. Therefore, it seems that migration from the releasing site begins unevenly. The postsmolts leading the way have already reached the southern Bothnian Sea in July–August (Fig. 3b) while a considerable number of postsmolts are still in the Bothnian Bay close the mouths of the home rivers. It is probable that those postsmolts still in home river areas are physiologically in such a condition that they are unable to start normal migration to the feeding areas. It is also possible that the smolt run or releasing time of hatchery-reared smolts and the sea surface temperature off the river mouth at the same time prevent postsmolt migration, because colder isotherms block the coastal area so that migration southwards means colder water temperatures. This is the case in early June (Fig. 4), but the situation changes rapidly when the coastal zone warms up and the isotherms form a thermal channel along which postsmolts can migrate within a stable or increasing temperature. In January–April tags have still been recovered along the coast when the majority of salmon are in their feeding grounds (Fig. 3e–f).

Power *et al.* (1987) have found that salmon smolts from the rivers draining into the Ungava Bay in Labrador descend to the sea in June and July when the temperature in the Ungava Bay is very low. Therefore, postsmolts stay in the estuaries until August when sea temperatures finally reach 2–4 °C. Postsmolts migrate out of the Gulf probably along the thermal channels, which are located near the shores. Dutil and Coutu (1988) reported that salmon postsmolts in the northern Gulf of St. Lawrence stayed for a long time in the nearshore areas from where they gradually left in late September. This movement out of the nearshore zone was associated with the decreasing near-surface temperature in autumn. Jutila *et al.* (2005) have hypothesised that a reduced survival of postsmolts is possible in years when the warming of the sea water is delayed.

Friedland *et al.* (1999) have suggested that these inshore habitats may serve not only as transit areas, but also as nurseries during the postsmolt growth season. According to Covey and Sargent (1979), growth increases with increasing water temperatures up to an optimum rate, thus



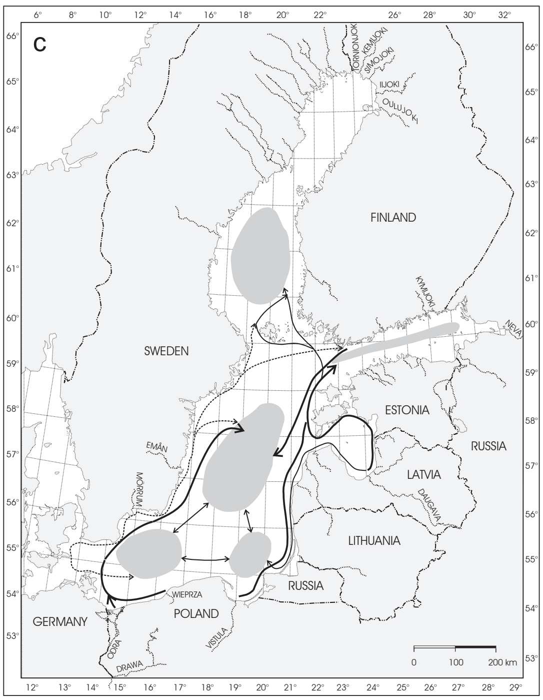


Fig. 5. Schematic map of the distribution patterns of postsmolts from the river mouths towards feeding areas. (**a**) Gulf of Bothnia rivers, (**b**) Gulf of Finland rivers, (**c**) Baltic Proper rivers.

making the postsmolt growth-survival mechanism temperature dependent. In the Baltic Sea during the smolt migration there is a temperature difference between inshore and offshore areas (Fig. 4). Therefore, for optimal growth and movement (migration), the best area is located inshore, where thermal channels are spread along the coastal zones.

Taking into account the food of postsmolts, which at the beginning of this migration phase mainly consists of airborne terrestrial insects (Lindroth, 1965; Power, 1969; Mitans, 1970; Jutila and Toivonen, 1985; Salminen *et al*., 2001), the availability of this food source is probably better closer to the coast than in offshore areas. The insectivory of postsmolts has also described by Brodeur (1989), who showed that airborne insects play important role as a first food of Pacific salmon species (*Oncorhynchus kisutch and O. tshawytscha)*. However, if suitable-sized prey fish are available, postsmolts feed on fish soon after entering the sea (Henking, 1916; Jutila and Toivonen, 1985; Salminen *et al*., 2001).

The isotherms, which run parallel to the coast line, provide a thermal channel to guide migration and simultaneously airborne terrestrial insects for food and probably also young herring, stickleback and sand eel. Salmon postsmolts are dependant of this kind of biotope until they are large enough to shift from an invertebrate-dominated diet to piscivory. It is probable that postsmolts entering from the Gulf of Bothnia to Baltic Proper migrate in the inshore area at least as long as they are dependant on small-sized prey. When postsmolts grow, the variety of edible food grows and postsmolt migration from the inshore area becomes possible. Hydro-acoustic tagging experiments have shown that in the offshore area the migrations of salmon are guided by movements of prey fish shoals (Andis Mitans, pers. comm. 2005, Latvian Fisheries Research Institute).

The salmon strains originating from the Gulf of Bothnia rivers normally migrate to feed in central and southern parts of the Baltic Proper (Christensen and Larsson, 1979; Ikonen and Auvinen, 1984). However, occasionally an extremely large proportion of postsmolts stop their migration in the southern part of the Gulf of Bothnia to feed (I, II), (Salminen *et al*., 1994; Kallio-Nyberg *et al*., 1999). The reason suggested for this behaviour was a strong availability of group 1 herring for postsmolts (II). This finding could be interpreted so that migrating postsmolts begin to feed on abundant 0+ herring and migration further to the Baltic Proper does not therefore take place. Salminen *et al*. (2001) have also shown that the tendency to migrate from the Bothnian Bay rivers to the Baltic Proper decreases when postsmolt size increases. They interpreted this finding as reflecting piscivory in the bigger postsmolts. When postsmolts switch to piscivory, the migration target has already been reached and therefore the need to migrate to Baltic Proper disappears and the migration is later directed by movements of prey fish. Salminen *et al*. (2001) have shown that salmon postsmolts sampled in the Bothnia Sea shifted from an invertebrate to a piscivorous diet when they reached a length of 300–319 mm (> 50% fish in diet). Thurow (1966) reported that salmon become piscivorous when they reach a size of 25 cm. However, it is plausible that when small enough prey fish are available for postsmolts, smaller postsmolts will also eat fish (Henking, 1916; Mitans, 1970; Jutila and Toivonen, 1985; Kallio-Nyberg *et al*., 1999).

Taking into account the size of wild smolts in the northern rivers (14–16 cm) (Saloniemi *et al*., 2004), the size should almost be doubled by feeding mostly on aerial insects before complete piscivory is reached. However, hatchery-reared smolts are normally bigger (mean length 17–19 cm) (I) than wild ones and therefore, the proportion of hatchery-reared fish feeding in the Bothnian Sea is larger than that of wild fish. Ikonen and Auvinen (1984) have shown that in the 1978–1982 smolt year classes the proportion of feeding salmon of hatchery-reared origin (Simojoki strain) caught in the Bothnian Sea was 27%, while the proportion of salmon of wild origin from the same strain was only 1.6%.

Alm (1934) has reported on salmon catches around Borholm and especially off the Polish coast, where directed fishing was developed to harvest small salmon (mean weight 0.8 kg). The freshwater age of these salmon was 3 or 4 years, which indicates that these fish originated from the northern rivers in the Gulf of Bothnia. The migration to the southern Baltic Proper must have been more or less continuous, probably without entering offshore areas to feed before reaching the southern Baltic Proper. The exiguity of salmon with a smolt age of one or two years (the Baltic Proper strains) in the same area was probably due to different direction of postsmolt migration. Tagging experiments (Mitans, 1970; Larsson and Persson, 1981; Bartel, 1987; Karlsson *et al*., 1995; Bartel, 2001) suggest the migration of Polish, Latvian and southern Swedish salmon towards the northern Baltic Proper, the Gulf of Finland and the Gulf of Bothnia.

4.1.2. Distribution of salmon from the rivers in the Gulf of Finland to the feeding areas

The salmon migration pattern detected in the Gulf of Finland (Fig. 5b) is based on tagging experiments with the Neva salmon strain, released into the Finnish rivers Kymijoki and Vantaanjoki (III). The salmon strain from the Neva River in Russia is used almost exclusively in all Finnish, Russian and Estonian smolt releases in former salmon rivers in the Gulf. Even in the rivers where small scale natural reproduction still exists, Neva salmon have been used in releases to enhance existing stocks.

For the Neva salmon strain, a short feeding migration is typical. When released into the Bothnian Sea, 95% of tag recoveries were obtained from the same sea area (Bothnian Sea), while for Iijoki salmon released into the same area only 50% were caught in the Bothnian Sea (III). When Neva salmon were released in the Gulf of Finland, 78% were caught in the same sea area (III). In the Gulf of Finland, the migration pattern of Iijoki salmon, Neva salmon and their hybrids were compared (Kallio-Nyberg *et al.*, 2000). This comparison suggested the longest feeding migration for Iijoki salmon and the shortest for Neva salmon. The hybrid of these strains migrated longer that the parental Neva strain, but shorter than the parental Iijoki strain. The observed differences confirm that the sea migration pattern is a stock-specific, inherited trait. Therefore, these salmon strains, which normally undergo a long distance feeding migration, can shorten the migration if suitable food is available at a closer distance. During evolutionary history, the migration to remote but stable feeding areas has guaranteed the survival of these salmon stocks. However, temporally existing feeding possibilities have always been utilized.

According to the tag recoveries of Neva salmon released in the 1980s as smolts into the Kymijoki River, the proportion of feeding salmon caught in the Gulf of Finland was 66% (Ikonen and Auvinen, 1984). However, since the mid-1990s the proportion has rapidly decreased and in 2000s the proportion has been 44%. Due to dramatically decreased postsmolt survival, offshore catches in the Gulf of Finland declined from about 20 000 salmon in the 1990s to 2000 salmon in the 2000s, which almost led to the ending of offshore fishing in the Gulf of Finland (ICES, 2005a). Simultaneously, smolt stockings have given very low catches in all fishing (ICES, 2005a). This is probably due to ecosystem changes in the Gulf of Finland, which have negatively affected the feeding possibilities of salmon postsmolts. Rönkkönen *et al.* (2004) reported that herring growth in the Gulf of Finland was exceptionally slow in 1986–1993. During the fast growth period in 1975–1980, *Pseudocalanus minutes elongatus* represented 43% the total zooplankton carbon content in zooplankton biomass, but only 11% when herring growth was slow. Ecosystem changes that have affected herring growth have possibly also affected salmon postsmolt survival.

A tagging experiment, in which River Neva and River Tornionjoki salmon (Bothnian Bay strain) were simultaneously released into the River Kymijoki, was carried out in 1998 and 1999. The tag recovery rate of the River Neva salmon was of 2–3%, while that of River Tornionjoki salmon was 12–15%. Feeding salmon of both strains were almost exclusively captured from the Baltic Proper (Ikonen and Saura, unpublished).

The lower recovery percentage of Neva salmon suggests that the postsmolts of this strain, with an innate tendency towards a short migration, cannot react to poor feeding conditions in the nearby area by migrating further to the Baltic Proper. However, a tagging experiment with Neva salmon smolts carried out in Norway in the River Akerselv draining into the Oslo Fjord suggested that one-year-old smolts (small) migrated after release from the fjord to the Atlantic Ocean, similarly to local salmon strains, but larger two-year-old smolts behaved similarly to those in the Baltic Sea, suggesting a short migration pattern (Hansen and Jonsson, 1991).

In the Gulf of Finland, the migration routes of salmon postsmolts are not known in detail. The Coriolis force circulates warmer Baltic Proper water along the southern coast to the east and along the southern edge of the archipelago off the Finnish coast to west. Therefore, the thermal channel can clearly be detected in the southern coast of the Gulf. Kazakov (1985) has shown that Estonian and Russian salmon postsmolts migrate along this channel to the east and then turn west, following the outer edge of the Finnish archipelago. Tag recoveries suggest that salmon from the Finnish Rivers in the Gulf of Finland also distribute along the edge of the archipelago. No clear migration along the coast has been detected, as occurs in the Gulf of Bothnia. Probably, due to the north to south directed currents (Tamsalu and Myrberg, 1995) and the close location of suitable feeding areas for postsmolts, Finnish salmon are distributed in nearby areas in the Gulf of Finland (Ikonen and Auvinen, 1985).

Migration from the Gulf of Finland to the Baltic Proper probably takes place later during the feeding phase, after the postsmolt stage (Ikonen and Auvinen, 1984). Hydro-acoustic tagging experiments have shown that feeding salmon follow the movements of the prey fish shoals (herring) (Andis Mitans, pers. comm., 2005, Latvian Fisheries Research Institute). Therefore, when herring migrate from the Gulf of Finland to the Baltic Proper (Aro, 1989) it is probable that a proportion of the feeding salmon follow this migration.

4.1.3. Distribution of salmon from the rivers in the Baltic Proper to the feeding areas

Salmon rivers with smolt production or smolt releases in the Baltic Proper are located in various parts of the Main Basin (Fig. 1). On the eastern side there are salmon rivers in the Gulf of Riga in Estonia and Latvia. On the eastern coast of the Baltic Proper, salmon smolt production also occurs in Latvian and Lithuanian rivers. In the south there are salmon smolt releases in Poland and in the south-western part of the Baltic Proper there are two salmon rivers in Sweden and small-scale smolt releases in Denmark (ICES, 2005a).

Gulf of Riga

In the Gulf of Riga rivers, smolts migrate to the sea in May (Mitans, 1970). Salmon postsmolts originating from these rivers remain for several weeks in the coastal zone of the Gulf before migrating out of the Gulf of Riga (Mitans 1969 ref. (Mitans, 1970). In the Gulf of Riga the offshore area warms later in the spring than coastal areas. Therefore, migration straight through the Gulf is not probable. Postsmolt migration follows the thermal channels close the coast. Depending on the location of sea entry, the postsmolts are at first distributed in the areas where the sea surface temperature is highest. During this phase the postsmolts feed almost exclusively on terrestrial airborne insects that have fallen onto the sea surface (Lindroth, 1961) or partly on small fish (Mitans, 1970). Therefore, during the time when postsmolts are totally dependent on terrestrial airborne insects or fish larvae encountered near the coast, the migration area is located in the vicinity of the coast. Especially at the time when smolts enter the sea, the surface temperature of the offshore areas is probably too low in all parts of the Baltic Sea for feeding and growth. Depending on the food available, postsmolts migrate along the thermal channels and thus distribute to areas that might be less favourable for the feeding of adult salmon.

After entering the Gulf of Riga the postsmolts migrate along the coastal zone to the north following the current. This has been observed when postsmolts have been caught as a by-catch in herring trap net fishing (Janis Birzaks, pers. comm. 2005, Latvian Fisheries Research Institute). There is a thermal channel leading out from the Gulf into north via Suurväina sound and Väinameri Sea between continent and islands of Hiiumaa and Saaremaa (Figs. 1 and 6). However, this area is crossed by a sill in which the water depth is only five metres (Suursaar *et al.*, 1998). Migration out to the north via Suur Strait and Väinameri Sea is probably not the main route, because despite intensive herring trap net fishing in this area, salmon postsmolts have seldom been taken as a by-catch in this fishing (Mart Kangur, pers. comm. 2005, Estonian Marine Institute).

The warmer water zone borders the northern coast of the Gulf of Riga in May, which leads out from the Gulf via Irben Strait (Fig. 1). Therefore, the most probable migration route for postsmolts out of the Gulf passes via the northern coast of the Gulf of Riga and northern part of the Irben Strait (Fig. 6). When migrating out of the Irben Strait,

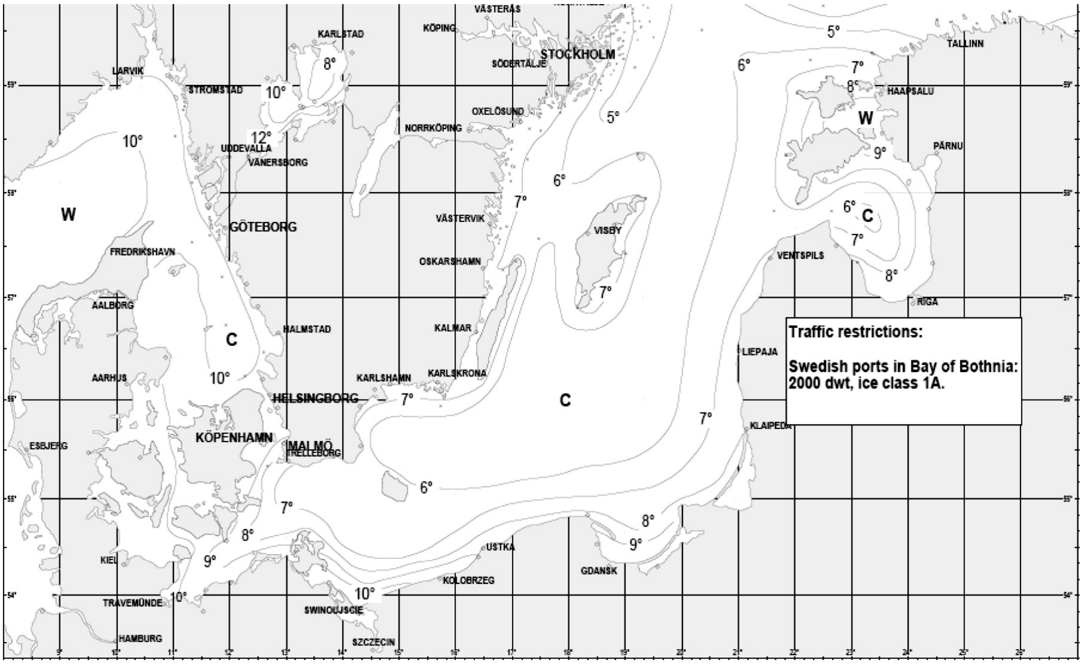


Fig. 6. Surface water temperatures in the Baltic Proper on 3 May 2004 according to the Swedish Meteorological and Hydrological Institute (SMHI, 2005).

postsmolts enter to thermal channel leading northwards to the Gulf of Finland. This hypothesis is supported by tag recoveries of Latvian salmon postsmolts obtained west of Saaremaa and Hiiumaa islands (Janis Birzaks, pers. comm. 2005, Latvian Fisheries Research Institute). Long-line catches in the Gulf of Finland suggest that the postsmolts migrate towards the north or northeast with the current (Fig. 5c). Tag recoveries also suggest migration to the Bothnian Sea (Karlsson *et al.*, 1995). However, the other migration route out of the Gulf of Riga could be along the southern coast and then out of the Irben Strait. Feeding fish recovered in the vicinity of Gdansk and Bornholm Deeps would suggest that migration to these areas had already taken place during the postsmolt phase. Alm (1934) has reported, on the basis of markings and hook findings, that in certain years Latvian salmon have been found to migrate to the south-western Baltic.

Polish coast

Salmon from the southern Baltic rivers in the Gulf of Gdansk (Poland) migrate towards northern Baltic Sea as far as to the Gulf of Finland (Bartel, 2001). This behaviour is similar to that of the Gulf of Riga salmon. At first the migration is anticlockwise following the current northwards to the Gulf of Finland, and from there salmon migrate back to the Baltic Proper (Fig. 5c). However, salmon originating from the rivers in south-western part of the Baltic Proper (River Drava and the rivers on the Pomeranian coast) seem not to have this anticlockwise migration pattern, but they spread out sporadically from the river mouth to the main feeding areas in the vicinity of the Gotland, Bornholm and Gdansk Deeps (Bartel, 1987; Bartel, 2001).

In tagging experiments (Bartel, 2001), smolts of the River Daugava salmon strain (Gulf of Riga river) have been released into the Rivers Drweca (Gulf of Gdansk), Wieprza (Pomeranian coast) and Drava (tributary of River Odra emptying into the Szczecin Lagoon). Tagged salmon smolts released in Drweca River were later caught in the mouth of Vistula River, in the Gulf of Gdansk and in the Gulf of Finland, whereas in Wieprza-released salmon were recovered in the area of Gotland Island. Salmon released into the Drava River migrated to the sea through the western part of the Szczecin Lagoon and also distributed to the Baltic Proper around Gotland Island (Fig. 5c). The migration pattern was almost similar to that found in the original Drawa salmon (Bartel, 1987).

The detected differences in the migration patterns of the Polish salmon strains have been attributed to the location of sea entry more than to the genetic background. Therefore, it can be hypothesised that environmental factors have affected the migration pattern. In May, the offshore area of the Baltic is still cold. As presented earlier, a thermal channel is formed from the Pomeranian coast to the Gulf of Finland, following the coastal areas of the east coast of the Baltic Proper. Therefore, postsmolts from the Gulf of Gdansk easily find this channel and probably use it as a migration route. However, salmon from the western Pomeranian coast and Sczcecin Lagoon find a suitable thermal area when migrating northwest and north. This channel leads postsmolts to the southern coast of Sweden and along the Swedish coast to the north. This conclusion could be drawn because there has been a concentration of tag recoveries around Gotland Island (Bartel, 1987; Bartel, 2001). Unfortunately Bartel did not report the gear used for catching tagged salmon. Therefore, it is uncertain whether these salmon were postsmolts.

Southern Sweden

There is only a little information available on the migration pattern of postsmolts of River Mörrumsån and River Emån salmon. On the basis of tag recoveries these Swedish salmon stocks mainly distribute to the Baltic Proper (Larsson and Persson, 1981), Lars Karlsson, pers. comm. 2005, Swedish National Board of Fisheries). Tag recoveries of River Emån salmon suggest a distribution to the Baltic Proper, but also to the Gulf of Bothnia and Gulf of Finland (Larsson and Persson, 1981). However, even though the best feeding areas of salmon are probably located just outside of the Rivers Mörrumsån and Emån, salmon seem to distribute to the northern Baltic Proper and the Gulfs (Fig. 5c). This migration probably also follows the thermal channel along the coast, as along the southern and eastern coast of the Baltic Proper. A northward migration from these southern areas has also been found in wide-migrating sea trout populations in southern Sweden and Poland. Svärdson and Fagerström (1982) have shown that tagged sea trout (*Salmo trutta* L.) smolts originating from the River Verkeån in southern Sweden distribute to the north-east from their home river as far as to the Gulf of Finland and Bothnian Sea. Bartel (1995) demonstrated that sea trout tagged and released off the Polish coast also migrate as far as the Gulf of Bothnia and Gulf of Finland. The southwards migration of salmon has also been detected with the aid of tag recoveries of River Mörrumsån salmon caught in the vicinity of Danish islands (Curt Insulander, 2005, pers. comm.).

Alm (1934) reported that in certain years (1925, 1930 and 1931) small salmon were caught along the coast of the Gulf of Bothnia and that these salmon had a lower age at smolt migration than those in the north Swedish rivers. Alm (1934) hypothesised that these salmon were partly from Norrland rivers, partly from the Estonian and Latvian rivers and maybe also from the rivers in southern Finland. However, Alm (1934) did not discuss the possibility that a proportion of these salmon could also have originated from southern Swedish rivers, which could nevertheless be as probable as Latvian salmon in the Gulf.

To conclude, salmon postsmolts from the southern Baltic Proper rivers migrate northwards along the coastal thermal channels in the same way as Gulf of Bothnia salmon migrate to the central and southern Baltic Proper. Polish and Latvian salmon migrate as postsmolts partly as far as the Gulf of Finland. The overall distribution of Emån salmon also suggests migration as far as the Gulf of Finland and Gulf of Bothnia. Unfortunately, no detailed data on the migration of River Mörrumsån salmon are available.

4.1.4. Spawning migration

Feeding periods last 1–3 years, sometimes even longer, before hormonal changes initiate the spawning run. The northern stocks begin their migration in the Baltic proper in March–April (Christensen and Larsson, 1979; Karlsson *et al.*, 1999a). From the offshore feeding areas the homing migration route is directed northwards and in May the migrating salmon are usually observed in the Åland Sea when they are captured by fishermen.

Salmon migrating to the rivers in the eastern and northern side of the Gulf of Bothnia follow the Finnish coast (Karlsson *et al*., 1996). However, salmon migrating to the rivers on the Swedish coast change sides in the Northern Quark, migrating from there either to the Bothnian Bay rivers or back to the south to the Bothnian Sea rivers on the Swedish side of the Gulf (Karlsson *et al*., 1996). Partly due to warmer Baltic Proper water entering the Gulf and partly due to climatic warming of inshore areas, a warm surface water layer is formed in the inshore area, especially along the eastern coast of the Gulf. Migration routes follow this warmest surface layer, or thermal channel, to the home rivers. Tagging experiments (temperature registering tags) of salmon during their homing migration suggested that they tend to migrate up the highest temperature gradient along the coast of Gulf of Bothnia (Westerberg *et al*., 1999). According to Westerberberg *et al*. (1999), the detected deviations to colder areas last only a short time or migrating salmon pass through a colder temperature gradient.

The importance of the thermal channel has also been noted by fishermen catching salmon by fixed trap nets. Gear has been placed across the thermal channel so that migrating salmon are guided into the gear.

The spawning migration routes in the Baltic Proper are not clearly defined before salmon enter to the coastal fishing area. Similar thermal channels can be detected in the inshore areas of the Baltic Proper to those described in the Gulf of Bothnia (Fig. 6). Homing salmon migrating to the Gulf of Bothnia enter the inshore area already in Baltic Proper and follow the thermal channel to the north. Karlsson *et al*. (1999b) have shown that migrating salmon tagged in the Stockholm archipelago (latitude 59°N), were later caught by coastal fishing in the Gulf of Bothnia. Therefore, they probably follow the same thermal channel along the coast along as postsmolts migrating in the opposite direction.

Another migration route of the northern salmon stocks from the Baltic Proper to the Gulf of Bothnia seems to pass via the Gulf of Finland, even via the eastern part of the Gulf of Finland. Tag recoveries, scale pattern analyses, as well as genetic studies utilising microsatellite techniques (Koljonen *et al*., 2005) have revealed that these migrating, northern salmon off the northern coast of the Gulf of Finland enter the coastal trap net fishery.

The homing pattern of Neva salmon released into the River Kymijoki is not as clear as the migration of salmon to the Gulf of Bothnia rivers. The catches from coastal trap net fishing suggest that in June the traps in the most western part of the Gulf catch earlier migrating salmon than more eastern traps. Later, catches decrease in the west and increase in east, suggesting migration along the northern coast of the Gulf to the home rivers. However, trap net fishing also takes place east of River Kymijoki. Salmon entering this fishery have probably migrated along the southern coast of the Gulf to the east and then north and west along the northern coast of the Gulf towards the home river. Salmon originating from Russian and Estonian rivers have seldom been caught in Finnish trap net fishing. This indicates that the migration route to these rivers follows the southern coast of the Gulf.

There are no data available to describe the homing of Latvian salmon to the Gulf of Riga. Tag recoveries only suggest that homing salmon are caught close to the releasing sites. Recoveries have not been obtained from the other parts of the Gulf (Karlsson *et al*., 1995). No data are available on the homing migration of Polish or Swedish (southern) salmon.

4.2. Food

Salmon food during the first months in the Gulf of Bothnia consists almost exclusively of terrestrial airborne insects that have fallen onto the sea surface (Lindroth, 1961; Jutila and Toivonen, 1985). Salminen *et al*. (2001) also found bottom fauna and small quantity of fish in addition to surface insects. In the Gulf of Riga, terrestrial insects formed about 75% of the weight of stomach content of postsmolts during the first weeks in the sea. The remainder mainly consisted of fish, i.e. Baltic herring larvae, young sandeels, and the little goby (*Pomatochistus minutus* Pallas). No fish larger than 45 mm were found in the stomachs of postsmolts (Mitans, 1970). In Norway, in Trondheim fjord, the stomach contents of postsmolts were dominated by adult insects (Levings *et al*., 1994; Andreassen *et al*., 2001). On the other side of Atlantic Ocean, in Ungava Bay, insects accounted for approximately 95% of the total food intake of postsmolts during the first months of the marine phase (Power, 1969).

According to Thurow (1966) salmon begin to eat fish in the Baltic Proper when they reach the size of 25 cm. Salminen *et al*. (2001) have shown that when salmon reach the size of about 30 cm in Gulf of Bothnia the majority of their food consists of fish, and when the length of salmon is 45 cm their diet is exclusively fish. However, the proportion of fish in the diet depends on the available prey size in relation to postsmolt size. Wankowski and Thorpe (1979) stated that salmonid fish show a high degree of prey selection based on body size. They also found that the maximum growth rate was achieved with only one size of prey item, termed the optimum prey size. Prey sizes larger and smaller than the optimum resulted in a reduction in growth rate, and often a loss in weight. Sturlaugsson (1994) has shown that postsmolts consumed prey of widths ranging from 0.3–4.7% of their fork length. Therefore, the availability of suitable-sized food affects the selection of feeding area (II), (Salminen *et al*., 1994; Kallio-Nyberg *et al*., 1999).

In papers IV and V it is shown that in the Baltic Proper in 1994–1997 sprat dominated in the salmon diet, followed by herring and on minor scale stickleback. In salmon smaller than 60 cm in length, 90% of the diet consisted of sprat and the rest was herring. In larger salmon (> 60 cm), sprat constituted 65% and herring 30% of the diet, and the remainder was stickleback. However, when compared to the food taken by salmon in 1957–1963 the share of sprat was greater (V). In the southern Baltic Proper the proportion of sprat was greater in January–April and May–September compared to the food of salmon caught in the eastern part of the Baltic Proper. In October–December sprat constituted 40–45% of the diet, herring the same proportion and the remainder consisted of stickleback.

However, in the northern Baltic proper (Lat 58°–59°30´N) in May–June 1995 the salmon diet contained 78% herring, 9% sprat, 12% stickleback and 1% sandeel and other fish (Ikonen, 1995). In an offshore sample from the Gulf of Riga, sprat did not exist in the salmon diet at all. The main food items were herring (50%), stickleback (45%) and other fish (5%) (V). The diet of salmon caught by offshore fishing in the Gulf of Bothnia consisted of about 70% herring together with sprat (10%) and stickleback (about 20%) (V). Salmi and Ikonen (1982) have shown that proportion of Baltic herring was 64% and the rest was sticklebacks in a sample of feeding salmon from the Bothnian Sea. In the Gulf of Finland in November 1973, salmon food consisted of herring (37%), sprat (24%), smelt (18.4%), stickleback (12.9%) and other fish (7.7%) (Andersson, 1980). In the Gulf of Gdansk, in the Puck Bay inside the Hel peninsula, salmon food consisted of Clupeidae fish (herring and sprat, 92.9%). The other species eaten were *Ammodytes* sp. and *Gasterosteus* sp. (Skora and Haluch, 2005).

During the homing run in the Gulf of Bothnia, herring accounted for 95% of the food of salmon and the rest consisted of sprat, stickleback and other fish, which all formed an equal share (V). Salmi and Ikonen (1982) found that during the spawning run, 91.9% of the diet was herring, 4.2% was smelt and sticklebacks formed 2.8% of the food (1.5% other food). However, the diet of homing salmon in the Gulf of Riga was quite different (herring 35%, stickleback 15%, and the remaining food consisted of other fish (perch *Perca fluviatilis* L., smelt *Osmerus eperlanus* (L.), sandeel *Ammodytes* sp., eelpout *Zoarces viviparous* L.)) (V). In the Baltic Proper the homing migration, which in all likelihood follows the coastal zone, probably also offers a diet that largely consists of herring. This is due to the behaviour of sprat, which predominantly occur in the offshore area.

In northern Norwegian waters, the salmon diet differs greatly from that in the Baltic Sea. The diet included lanternfish, *Myctophidae*, squid, capelin, *Mallotus villosus,* amphipods and euphasids (Thurow, 1973). Hansen and Pethon (1985) found that off the coast of northern Norway the most important food items were euphasids and hyperid amphipods as well as myctophid *Benthosema glaciale*, and squid *Gonatus fabricii*. They also found that the type of food did not appear to be related to the length of fish. According to Hansen and Pethon (1985) in coastal waters off West Greenland Labrador, the important prey species of salmon were found to be capelin, sand eel, herring, barracudina, *Paralepis coregonoides borealis,* amphipods, euphasids and squid. In the north-east Atlantic, salmon fed mainly hyperid amphipods, euphasiids, shrimps, lanternfish, pearlsides and barracudinas, and to a lesser extent on larger fish and squid. Crustaceans, including *Themisto* sp. euphasiids and shrimps, accounted for 95% of the food in number, but only about 30% by weight (Jacobsen and Hansen, 2001).

When comparing the diet of salmon between the Baltic Sea and Atlantic, similarities have mainly been found during the early postsmolt phase, with a dominance of insects. However, Lacroix and Knox (2005) have reported that in the diet of postsmolts caught in the Bay of Fundy, terrestrial insects and freshwater invertebrates were almost absent. The authors reported that postsmolts had made the transition from a habitat of feeding on surface drift to one of pelagic foraging by the time they reached the outer Bay of Fundy. In the Baltic Sea the postsmolts probably feed for longer in the inshore area with a diet consisting of terrestrial insects and young herring and sandeel, because in the offshore area there is a scarcity of suitable-sized food. During the later postsmolt phase and after it the di*et al*so differs considerably. In the Baltic Sea it consists of sprat, herring, stickleback and sandeel, while in the Atlantic crustaceans play important role in addition to various fish species and squids.

4.3. Detection of M74 syndrome in wild and hatchery reared salmon populations

In the hatchery-rearing of salmon, in which eggs have been taken from the feral spawners ascending the river, the effects of M74 mortality have easily been detected (I), (Norrgren *et al*., 1993; Börjeson *et al*., 1994; Amcoff, 2000). However, in nature, the effects of the syndrome are more difficult to detect. Electro-fishing surveys indicate parr densities in rivers, but the reasons for variations in parr densities are often difficult to determine. In the River Tornionjoki the poor year class of 1992 was attributed to the M74 syndrome on the basis of electro-fishing surveys (Soivio, 1995; Karlström, 1999; ICES, 2005b). Therefore, the spawning migration arising from this year class in 1997 was expected to be relatively poor. However, the spawning run in 1997 was strong. Ageing of migrating spawners revealed that the expectation of a poor spawning run of the 1992 year class was correct, but it was masked by the strong year class of 1991, which also produced an exceptional number of four-year-old smolts (VI). These salmon dominated in the run in 1997 and the proportion of fish from the year class of 1992 in the run was as poor as expected (VI).

In hatchery practices it is possible to obtain enough rearing material by incubating surplus eggs and thus avoid problems caused by exceptionally high fry mortality. In the Finnish hatchery practices, which only utilise captive spawners, the M74 syndrome had no effect. These spawners were fed with man-made feed, which included practically no components from the Baltic Sea, and the vitamin status of this artificial feed was balanced to the optimal level. The strong year class of 1991 in natural populations provided such a large number of ascending spawners, originating from a healthy year class, that in coastal catches the effects of M74 syndrome were not visible. However, in most of salmon rivers in the Gulf of Bothnia and in the River Mörrumsån in the Baltic Proper a decrease in parr densities was found during the years when syndrome-related fry mortality was high in 1992–1996 (ICES, 2005b).

During the most recent years, the number of feeding fish has been small in the Bothnian Sea. The fact that the majority of the fish are feeding in the southern Baltic Proper suggest small numbers of M74-positive salmon females in northern populations. Hatchery observations, experimental salmon egg incubations as well as parr density findings also suggest low M74-mortality both in wild and reared populations.

The situation within the Gulf of Finland populations is similar, and there have been few salmon feeding in the Gulf. The yolk-sac-fry mortality caused by the M74 syndrome is also on a low level (ICES, 2005a). In the Baltic Proper, where

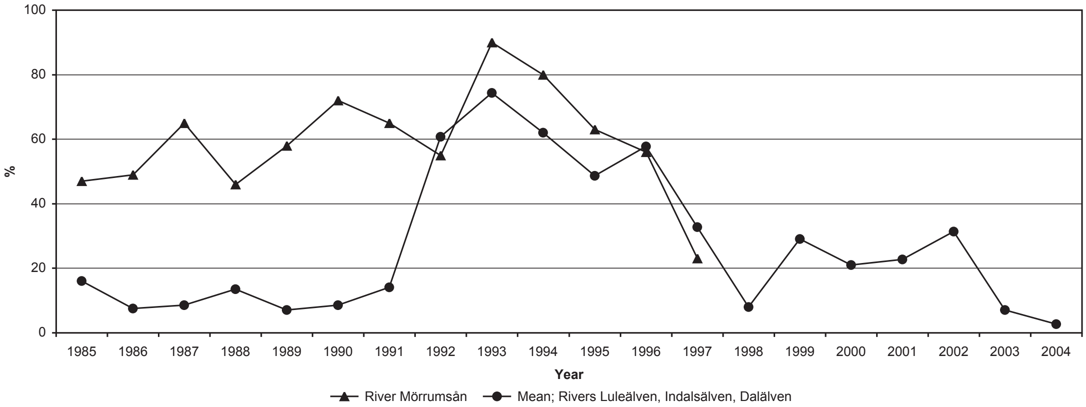


Fig. 7. The M74 frequency or the mean offspring mortality of sea-run spawners in hatching years 1985–2004 according to (ICES, 2005b).

the syndrome has only been detected in the River Mörrumsån, no data have been available since 1998. However, I would like to point out that the prevalence of the syndrome in salmon entering the River Mörrumsån was around 50–70% in 1985–1991, while the proportion of M74-positive female salmon was well below 20% in the salmon populations in the Gulf of Bothnia (Fig. 7). In 1993 the prevalence of the syndrome peaked in the River Mörrumsån, when it was also high in the Gulf of Bothnia salmon populations. From 1993 until 1997 the proportion of M74-positive female salmon declined in the northern salmon strains. Unfortunately, there are no further data that would show whether the mortality rates due to the syndrome have also decreased in the River Mörrumsån, as in all other sampled rivers No mortality caused by M74 has been recorded in Latvian salmon (Koski *et al*., 2001; ICES, 2005b) (Janis Birzaks, pers. comm. 2005, Latvian Fisheries Research Institute) or in Polish hatcheries (ICES, 2005b) (Ryszard Bartel, pers.comm. 2005, Inland Fisheries Institute, Poland).

5. Conclusions

5.1. M74 and feeding migration

5.1.1. Gulf of Bothnia salmon

The salmon strains from the Gulf of Bothnia rivers normally migrate to the Baltic Proper during the postsmolt phase to feed. Migrations within the Baltic Proper mainly relate to the movements of prey fish shoals. Feeding salmon stay in Baltic Proper until the spawning migration begins.

Occasionally, when postsmolts encounter exceptionally favourable feeding conditions (abundant 0+ herring) during their migration in the Bothnian Sea, a large proportion of migrating salmon stop their migration out of the Bothnian Sea to the Baltic Proper and remain in the Gulf until they are ready to start the spawning migration.

Larger postsmolts, mostly of hatchery origin, more often remain to feed in the Bothnian Sea. Due to their greater size, the variety of food available to them is wider than for smaller smolts and further migration to the Baltic Proper is therefore not obligatory.

In the Baltic Proper the main feeding areas of the northern salmon strains are located in the vicinity of the Bornholm, Gdansk and Gotland Deeps. In these areas the main food component is sprat, and less important food items are herring, stickleback and sandeel.

In the Bothnian Sea, herring play the main role as prey species followed by stickleback, while the role of sprat is negligible. The food available in the northern Baltic Proper mainly consists of herring and to some extent of sprat and stickleback The northern Baltic Proper (north of L 58°30´N) is less important as a feeding area and the Gulf of Finland and Gulf of Riga are not used at all as feeding areas for the northern salmon strains.

The tag recovery data and catch statistics indicate that the increased abundance of feeding salmon in Bothnian Sea and probably also in the northern Baltic Proper was followed by an increased proportion of M74-positive female salmon in the rivers of the Gulf of Bothnia.

5.1.2. Gulf of Finland salmon

The Neva salmon, which is the most common strain in the Gulf of Finland and a genetically more local strain compared to salmon in the Gulf of Bothnia, appears to be dependant on feeding grounds in the Gulf during the postsmolt phase. When piscivorous, migrations of Neva salmon out of the Gulf are common, probably following shoals of the main prey species, the herring, which migrates between the Gulf of Finland and the Baltic Proper. Therefore, some of the Neva salmon feed in the Gulf and others in the Baltic Proper. There the main feeding area is in the vicinity of Gotland Deep, where the salmon diet is dominated by sprat. In the northern Baltic Proper, herring plays a major role in the diet, while the share of sprat in the diet varies according to the status of the sprat stock. During periods when the sprat stock is strong, this species is also more common in the northern Baltic Proper.

The M74 syndrome has also existed in the Gulf of Finland but has not affected the salmon populations as strongly as in the Gulf of Bothnia. The feeding of salmon originating from the Gulf of Finland has partly taken place in the Gulf, where the diet has predominantly consisted of herring and stickleback and to lesser extent of sprat. A certain proportion of the salmon migrate to the northern Baltic Proper, where herring is also the most important prey species, followed by stickleback and sprat. However, tag recoveries also suggest migration to more southern areas. Due to the dual feeding behaviour, salmon feeding in the Gulf of Finland and in the northern Baltic Proper probably include a greater proportion of M74-positive female salmon than those feeding in the Baltic Proper. Since the late 1990s the proportion of salmon feeding in the Gulf has been small, as also has the number of M74-positive females.

5.1.3. Baltic Proper salmon

According to tag recoveries, Latvian salmon have four main feeding areas: the Gulf of Finland, Gotland Deep, Bornholm Deep and Gdansk Deep. No information is available on how permanently salmon feed in the Gulf of Finland. However, it is known that a certain proportion of postsmolts migrate to the Gulf and feed there at least until they recruit to long line fishery out in the Gulf. The main prey species there are herring and stickleback and to some extent also sprat. Whether they migrate later during feeding period out of the Gulf is not known. Nevertheless, feeding salmon originating from the Latvian rivers in the Gulf of Riga have also been observed to feed in the vicinity of Gotland, Bornholm and Gdansk Deeps. The Gulf of Riga plays no role as a feeding area for salmon.

Salmon from the Polish coast originating from the River Drava, which is a tributary of the River Oder, migrate to feed in the vicinity of Gotland Island. Southern feeding areas, the Bornholm Deep and Gdansk Deep, are less important for Drava salmon than for salmon from the Gulf of Bothnia. The main prey species, according to the feeding area, are likely to be sprat and herring.

Tagged Daugava salmon (Latvian origin) released into the Gulf of Gdansk rivers were more often caught in the Gulf of Finland and Gulf of Gdansk than those (of the same strain) released into rivers draining more westwards on the Polish coast. The latter group, however, yielded more recoveries from areas east of Bornholm Island. Most Polish salmon were thus mainly feeding on sprat in the Baltic Proper area, but those that migrated to the Gulf of Finland and northern Baltic Proper probably fed predominantly on herring. Unfortunately, due to the shortage of data, it is not known how permanent these northern feeding areas are for Polish salmon. They might enter these northern areas during the postsmolt phase but gradually migrate to more southern areas. However, catch samples collected in the Bornholm Deep area and Gulf of Finland suggest that Daugava salmon occur in the Gulf of Finland samples but not in those from the Bornholm Deep.

Salmon originating from the eastern and southern Baltic Proper (Latvia and Poland), have not suffered from the M74 syndrome. A certain proportion of salmon from the rivers in these areas have been shown to feed in the Gulf of Finland and therefore, if the syndrome is induced by the feeding area, there should be M74-positive female salmon in the spawning populations. However, a possible explanation for the absence of the syndrome is that the Gulf of Finland is not the permanent feeding area for these salmon, but they gradually migrate to the Baltic Proper before their spawning run. Therefore, their herring/stickleback diet will change to one dominated by sprat before the spawning run.

The salmon strains from the south-western part of the Baltic Proper (Rivers Mörrumsån and Emån) migrate all over the Baltic Proper and also in the Gulf of Finland and Gulf of Bothnia. Due to the limited data available, it is difficult to estimate the relative importance of the northern Baltic Proper, Gulf of Finland and Gulf of Bothnia as feeding areas for these strains. Individuals migrating in the north probably feed mainly on herring and stickleback, while those in the more southern areas probably feed mainly on sprat.

The occurrence of the M74 syndrome in the River Mörrumsån is difficult to explain.. Based on weak evidence that salmon from the River Mörrumsån migrate to the northern Baltic Proper as well as the Gulfs of Finland and Bothnia, it could be hypothesised that the proportion of salmon feeding in the northern Baltic Proper and in the Gulfs (mainly herring) has annually been so high that it has resulted in an increase in the number of M74-positive females in spawning populations.

5.2. M74 and food

In papers IV and V it was demonstrated that the incidence of M74 syndrome positively correlated with an increased abundance of sprat. However, the M74 syndrome was not detected in the Baltic Proper salmon strains in Latvia and Poland, which mostly feed in the areas where the sprat dominates as the prey species. Additionally, it was stated that M74 occurs in a salmon stock (Neva salmon) that is resident in the Gulf of Bothnia, although the sprat does not occur in that area.

The salmon diet in the southern and central Baltic Proper is dominated by Clupeids. Sprat is the most important prey species followed by herring, stickleback and sand eel. However in the northern Baltic Proper salmon feed mainly on herring.

In the Gulf of Finland the main food items are herring and stickleback and to some extent sprat, and in the Bothnian Sea salmon feed mainly on herring and to a lesser extent on stickleback. The ultimate reasons why salmon feeding in the northern waters seem to suffer from the M74 syndrome are still open, but a diet dominated by herring is probably one of the contributing factors.

A deficiency of thiamine has been demonstrated to be the main factor in the etiology of the M74 syndrome, as well as the Early Mortality Syndrome (EMS) in the Great Lakes and the Cayuga Syndrome in the Finger Lakes in New York State. The shortage of thiamine may be induced by the presence of thiaminase, an enzyme capable of destroying thiamine, in prey species. A higher thiaminase activity has been demonstrated in herring than in sprat, at least in the northern Baltic Sea. There is also evidence suggesting that at least during certain periods and in certain areas the thiamine concentration of sprat is perhaps more than twice that in herring. However, some analyses suggest that the thiamine concentration is in herring higher than in sprat. Unfortunately, no comparative analyses are available showing the thiamine content of herring and sprat in the different feeding areas of salmon. However, the thiaminase activity of salmon forage fish, at least herring, may be a possible link in the etiology of the M74 syndrome.

It is also possible that the causative factor of the M74 syndrome, which seems to arise from salmon feeding in the northern Baltic Sea, is probably not a question of the prey fish species but the quality of the prey fish. Unfortunately, there is no exact information on where the M74-positive female salmon have been feeding. However, the positive relationship between the M74-positive female salmon in the northern stocks and the proportion of fish feeding in the Bothnian Sea in the previous year suggests that M74 is related to the northern feeding areas.

The egg and muscle colour of M74-positive female salmon was paler than that of M74-negative salmon, suggesting a different food supply. Additionally, higher concentrations of dioxin-like organochlorines were detected in the muscles of the M74-positive female salmon compared to healthy ones. The lower dioxin content of healthy salmon spawners was probably due to their feeding in the southern Baltic Proper, where the dioxin content of herring and probably also of sprat may be considerably lower than in those fish feeding in the northern areas.

The shortage of carotenoids in the M74-positive females is probably related to food web differences between separate feeding areas. In the southern Baltic Proper the food web of salmon consists mainly of sprat and herring that have fed on neritic zooplankton species such as *Temora, Pseudocalanus* and *Centropages*. In the northern areas the salmon diet consists mainly of herring. The food available to herring in the northern Baltic Sea was found to be mainly smaller limnic zooplankton such as *Eurytemora, Acartia* and *Limnocalanus*.

The pale eggs and less pigmented muscle colour of M74-positive female salmon is probably due to feeding in the northern Baltic Sea. Salmon obtain astaxanthin via crustaceans eaten by salmon prey species. Crustaceans in the Baltic Sea are not normally directly preyed on by salmon, because all crustaceans available in the Baltic Sea are too small for feeding salmon. Therefore, salmon take crustaceans indirectly via prey fish species. The neritic plankton species offer a better source of astaxanthin compared to limnic ones. Therefore, it seems plausible that well-pigmented salmon in the spawning populations are those that have fed in the southern Baltic Proper utilising a food web in which at least *Temora* is one source of carotenoids. Fish can acquire thiamine via crustaceans. If the neritic crustaceans contain more thiamine than limnic ones, the thiamine deficiency in M74 spawners could also be explained.

The less rich food available in the northern areas compared to the Baltic Proper probably resulted in the lowest condition factor of herring being detected in the Baltic Sea. Grazing on smaller prey species in the Bothnian Sea is more difficult and gives less energy compared to larger neritic plankton species in the Baltic Proper. The condition factor of salmon feeding in the Bothnian Sea was also lower than in those feeding in the Baltic Proper.

I have shown that the proportion of feeding salmon in the Bothnian Sea is positively related to the size of the herring year classes. A good availability of young herring for migrating postsmolts has halted postsmolt migration in the Bothnian Sea, which has resulted in an increased number of feeding salmon in that area. If the food resources in the Bothnian Sea are limited for the average size of herring year class, it is possible that a strong herring year class can graze food resources to a level that further lowers the condition factor. These herring suffering from a shortage of food, when eaten by salmon, provide a lower nutritive value in the salmon food. Therefore, during those years when larger numbers of salmon are feeding in the Bothnian Sea, it is possible that the food quality is even worse than on average. The low fat content of the diet may affect not only the caloric intake but also the thiamine requirement. Therefore, fish on a high-fat diet might take longer to develop deficiencies.

Salmon feeding in the Gulf of Finland and probably also those feeding in the northernmost Baltic Proper have probably been affected by a similar mechanism. Due to the decreased salinity in the Baltic Sea, the abundance of neritic species of zooplankton has decreased and the limnic ones increased in the Gulf of Finland and northern Baltic Proper. Therefore, the diet available for salmon prey species resembles that in the Bothnian Sea. The food quality available for salmon, feeding only in northern Baltic Proper and Gulf of Finland, probably also resembles that available in the Bothnian Sea. Therefore, M74-positive female salmon occur in the Gulf of Finland spawning populations. It is also possible that the M74 syndrome detected in the River Mörrumsån is related to feeding in northern waters of the Baltic Sea.

5.3. M74 in wild and hatchery-reared populations

The observations presented above suggest that salmon migrating in the Bothnian Sea, the Gulf of Finland and probably also in the northern Baltic Proper and feeding mainly on herring suffer from the M74 syndrome. Wild salmon smolts originating from the rivers in the Gulf of Bothnia mainly migrate into the central and southern Baltic Proper to feed. Hatchery-reared smolts from the Gulf of Bothnia also migrate to the same areas, but a greater proportion select the Bothnian Sea for feeding. This has been explained to be related at least to the larger smolt size originating from the compensatory releases. Therefore, I would like to conclude that because most feeding salmon in the Bothnian Sea are of hatchery origin, M74-positive salmon should therefore be more common within hatchery-reared populations than in wild populations. However, when exceptionally good feeding possibilities are available in the Bothnian Sea, a greater proportion of wild postsmolts then also stay in the Bothnian Sea and feed there until they begin their homing.

In the Gulf of Finland there are too little data on migration differences between wild and hatchery-reared smolts to estimate the occurrence of M74-positive females in these populations of different origin. The same applies to the salmon strain in the River Mörrumsån.

5.4. Looking to the future

The findings presented above suggest that the M74 syndrome was probably related to the feeding migration and diet of salmon in the Bothnian Sea, the Gulf of Finland and in the northernmost Baltic Proper. Therefore, if the main causative factor in the etiology of M74 is a predominance of herring in the diet and the thiaminase enzyme within herring, the M74 syndrome should also occur in the future. Therefore, it is probable that an increased abundance of feeding fish in the area where herring dominates in the diet may also in the future give rise to an increased proportion of M74-positive female salmon in spawning populations. However, if the M74 syndrome is related to the food web of salmon prey species, the situation might be different. The improved condition of prey fish species due to changes in the food web caused by an alteration in the ecosystem might lead to decreased M74 mortality, even though the feeding areas do not change.

Preliminary findings reported by fishermen suggest that salmon long-line catches in the Gulf of Finland in autumn 2005 had evidently improved from those in the late 1990s and early 2000s, suggesting an increased abundance of feeding salmon in the Gulf. These findings might mean that the ecosystem has changed in a positive direction for salmon postsmolts and feeding salmon. There are also preliminary observations that herring year classes of 2004 and 2005 are probably stronger than previously. Additionally, the abundance of sprat in the Gulf has increased. Both herring and sprat have been reported to be in good condition, suggesting adequate feeding possibilities. Unfortunately, there are no analysed data supporting these findings at present.

I have hypothesised in this thesis that salmon from the Gulf of Finland rivers would probably suffer from the M74 syndrome due to feeding in the Gulf of Finland and in the northern Baltic Proper. This hypothesis concerned a period when herring growth at age, as well as the condition factor, were probably worse than in Autumn 2005. However, the present, preliminary findings suggest that herring in the Gulf of Finland are no longer starving and sprat are also abundant in the Gulf. Therefore, it is possible that the nutrition of the feeding salmon has changed so much that the available diet includes enough thiamine to prevent the occurrence of the M74 syndrome. However, the situation will be seen in salmon hatcheries or in experimental incubation studies no earlier than in spring 2007 when the eggs hatch.

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